

THE LATE PALAEOZOIC BRACHIOPOD GENUS *YAKOVLEVIA*
FREDERICKS, 1925 AND THE *YAKOVLEVIA TRANSVERSA* ZONE,
NORTHERN YUKON TERRITORY, CANADA

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The familial and superfamilial position, relationship with *Muirwoodia* Likharev, species composition, and stratigraphical and palaeogeographical distribution of *Yakovlevia* Fredericks are reviewed. *Muirwoodia* is considered to be a junior subjective synonym of *Yakovlevia*, which is placed in the Yakovleviidae Waterhouse within the Linoproductacea Stehli. Forty-five described (and/or illustrated) species ranging from the Middle Carboniferous to the mid-Permian (Wordian/Kazanian) from the Arctic, northeast China, Russian Far East, Japan, western North America, southwest United States, and Mexico are assigned to *Yakovlevia*. The palaeogeographical implications of the occurrences of the genus in northeast China, Japan, and United States–Central America is discussed. The *Yakovlevia transversa* Zone, most likely of Early Sakmarian (Tastubian) age, here established is based on material from the Jungle Creek Formation, northern Yukon Territory, Canada, and is correlated with several other faunas in the Arctic and western North America. *Yakovlevia transversa* (Cooper) is also described based on the Canadian material.

THE LATE PALAEOZOIC brachiopod productid genus *Yakovlevia* Fredericks (1925) is among the more characteristic brachiopod genera that distinguish the Late Palaeozoic Boreal Realm from the Tethyan and Gondwanan Realms to the south (Ustritskiy 1961; Shi & Waterhouse 1991). Biostratigraphically and palaeobiogeographically the genus is of particular interest because of its relatively short stratigraphical range, distinctive morphological characteristics, and restricted occurrences to the Northern Hemisphere [its occurrence in Chile recorded by Minato & Tazawa (1977) as *Muirwoodia* sp. is herein regarded as belonging to *Duarteia* Mendes (1959), see discussion below]. The *Yakovlevia transversa* Zone recorded in this paper is traceable at many localities in the Arctic region and thus appears to represent a distinct time horizon of the Early Permian for the Boreal Realm.

Although *Yakovlevia* has been described since 1925, and the genus is morphologically distinctive, its systematic position is still a matter of debate. So far, it has been assigned to six different families: Productidae Gray, Paucispiniferidae Muir-Wood & Cooper, Retariidae Muir-Wood & Cooper, Anidanthidae Waterhouse, Linoproductidae Stehli, and Yakovleviidae Waterhouse. In addition, the relationship of *Yakovlevia* with *Muirwoodia* Likharev (1947) is still subjected to various opinions despite the earlier definitive study by Kotlyar (1961) who clearly showed that the two were not significantly different.

From 1988 to 1991, the author (Shi 1991) studied a large collection of Lower Permian brachiopods and molluscs from northern Yukon Territory, western Canada, among which there were well preserved specimens of *Yakovlevia transversa* (Cooper 1957) (see description later in the paper). The bulk of my thesis has been submitted to the Geological Survey of Canada for publication. The present paper provides a review of *Yakovlevia* based on the Canadian material, including discussions on its systematic position, its relationship to *Muirwoodia* and other related genera, and its stratigraphical and palaeogeographical distributions. Additionally, the paper also establishes *Yakovlevia transversa* Zone of the Sakmarian age based on material from the northern Yukon Territory of Canada, and attempts to correlate this zone with coeval faunas from North America and the Arctic. The species *Y. transversa* Cooper is also described and illustrated based on the Canadian collections.

The fossils described in this paper are registered by the prefix GSC and housed in the type collections of the Geological Survey of Canada, Ottawa. Two sets of locality numbers are used herein, one prefixed with GSC loc. with a five-figure serial number, representing fossil collections made by the officers of the Geological Survey of Canada, Dr E. W. Bamber in this case, and the other prefixed with JBW loc. with a two-figure serial number, representing collections made by Professor J. B. Waterhouse and colleagues during

expeditions to the study area between 1968 and 1972. Both field locality numbers are now registered with the Geological Survey of Canada, and the locality details have been provided by Waterhouse & Waddington (1982, Appendices 2 and 4).

RELATIONSHIP OF *YAKOVLEVIA* WITH *MUIRWOODIA*

Yakovlevia was proposed first as a subgenus of *Chonetes* Fischer de Waldheim by Fredericks (1925, p. 7) with the following description: 'Shell concavo-convex, productid-like, with area (interarea) in ventral valve. Ventral interior probably with development of apical plates and usually filled by secondary shell substance; anterior end of the apical plates extend forwards as well-developed ridges to enclose strongly depressed muscle field. Presence of a (ventral) median septum is not known.' The type species, *Y. kaluzinensis* Fredericks (1925), is represented only by ventral internal moulds, in which a high, about 3 mm across, transverse band is well shown along the hinge line (Fredericks 1925, pl. 2, figs 64-66). In establishing this subgenus Fredericks noted the strong similarity of *Y. kaluzinensis* to productid shells, especially *Productus mammatus* Keyserling (1846).

Fredericks' diagnosis of *Yakovlevia*, particularly the presence of an 'interarea' with 'apical plates', was accepted by Likharev (1947), who subsequently proposed *Muirwoodia* for *Productus mammatus* Keyserling, chiefly on the basis that it has a thickened marginal area instead of an interarea with a median delthyrium supposedly characteristic of *Yakovlevia*. In their study of Productida Gray, Muir-Wood & Cooper (1960) also recognised *Muirwoodia* on similar accounts, but their conclusion was primarily based on observations on material from the Glass Mountains, West Texas, which they then regarded as *Muirwoodia* spp., but it should be noted that these Texas *Muirwoodia* spp. are now all placed in *Yakovlevia* by Cooper & Grant (1975) and the entire genus treated as a junior synonym of *Yakovlevia*. Other authors have also recognised *Muirwoodia*, wittingly or unwittingly (e.g. Dunbar 1955; Kashirtsev 1959; Gobbett 1964; Likharev & Kotlyar 1978; Kalashnikov 1980; Abramov & Grigor'yeva 1983; Duan & Li in Ding et al. 1985; Liu & Waterhouse 1985; Nakamura et al. 1987; Lazarev 1990).

Kotlyar (1961), on the other hand, critically examined the alleged presence of an 'interarea' and a 'delthyrium' in *Yakovlevia* based on more material and concluded that the so-called interarea was in reality 'none more than a thickened hinge margin which B. K. Likharev called "a marginal

area".' Kotlyar subsequently treated *Muirwoodia* as a junior subjective synonym of *Yakovlevia*. Similarly, Sarycheva et al. (1960), Likharev (1960, p. 484), Mironova (1964, 1967), Barchatova (1970), Stehli & Grant (1971), Ustritskiy (1971), Zavodovskiy & Stepanov (1971), Ifanova (1972), and Cooper & Grant (1975) have also considered the two to be synonymous. Grant (in Brabb & Grant 1971) effectively suppressed *Muirwoodia* by placing its type species, *Productus mammatus*, in *Yakovlevia*. Cooper & Grant (1975) described the thickened hinge margin as a ginglymus (Fig. 1A), which they showed among their excellently preserved *Yakovlevia* from West Texas to be highly variable, suggesting that its formation is probably not genetically controlled but more probably an ecologically motivated feature. The ginglymus is not observed among the Canadian material as most of the specimens studied are either external or internal moulds, or separate valves.

In addition to the ginglymus, the hinge area of the ventral valve of *Yakovlevia* is usually marked by a well-demarcated transverse band just below or anterior to the gylingmus (see Fig. 1). Unlike the gylingmus which never reaches the cardinal extremities (Fig. 1A), the transverse band extends for the entire width of the hinge margin and, in some specimens, swings across the inner ears into lateral margins as low, flattened ridges that are often marked by striae (Figs 1B and 1C). On separate internal moulds of *Yakovlevia* from Yukon Territory, the transverse band is well preserved in many specimens of ventral valves and marked by small, irregularly spaced tubercles (pits on internal moulds) (Fig. 1B). An identical transverse band along the hinge area of dorsal valves is also observed in the Canadian material and marked by tubercles (dimples on internal moulds) corresponding to pits on the ventral valves (Fig. 1C).

The function of the gylingmus, the transverse band, and the embedded pits and tubercles in *Yakovlevia* is not clear, but Cooper & Grant (1975) suggested that they may be related to helping with the articulation of these transverse shells.

The alleged presence of apical plates and a delthyrium in the ventral interior of *Yakovlevia* is clearly a misinterpretation, judged from observations on the Canadian material as well as examination of the illustrations of *Yakovlevia* from Texas by Cooper & Grant (1975). One of the most conspicuous features that characterise *Yakovlevia* is its large, broadly heart-shaped muscle field on the posterior floor of the ventral interior (Figs 1B and 1C). The diductor sears are large, flabellate and deeply striate, separated anteriorly by a

thick, narrow platform which decreases in height posteriorly. The adductor scars are located between but posterior to the diductor scars and posteriorly separated from the latter by a layer of smooth callus that covers much of the posterior part of the diductor scars (Fig. 1A). The whole muscle field is posteriorly located, deeply depressed, and encircled by strongly developed shell thickening, which in many specimens is strongly elevated and extends posteriorly right into the beak, therefore making a false impression of a delthyrium and apical plates under the beak and the ginglymus (Figs 1A and 1B).

Apart from the misinterpretation of the thickened hinge margin (and ginglymus) and the posterior extension of the deeply depressed ventral muscle field, other internal structures of both *Yakovlevia* and *Muirwoodia* have been considered to be essentially the same by many authors (Muir-Wood & Cooper 1960; Kotlyar 1961; Abramov & Grigor'yeva 1983). Thus, in view of the above observations and interpretation I suggest we follow Kotlyar (1961) and Cooper & Grant's (1975) conclusion that *Yakovlevia* and *Muirwoodia* are synonyms and the latter be suppressed as a consequence.

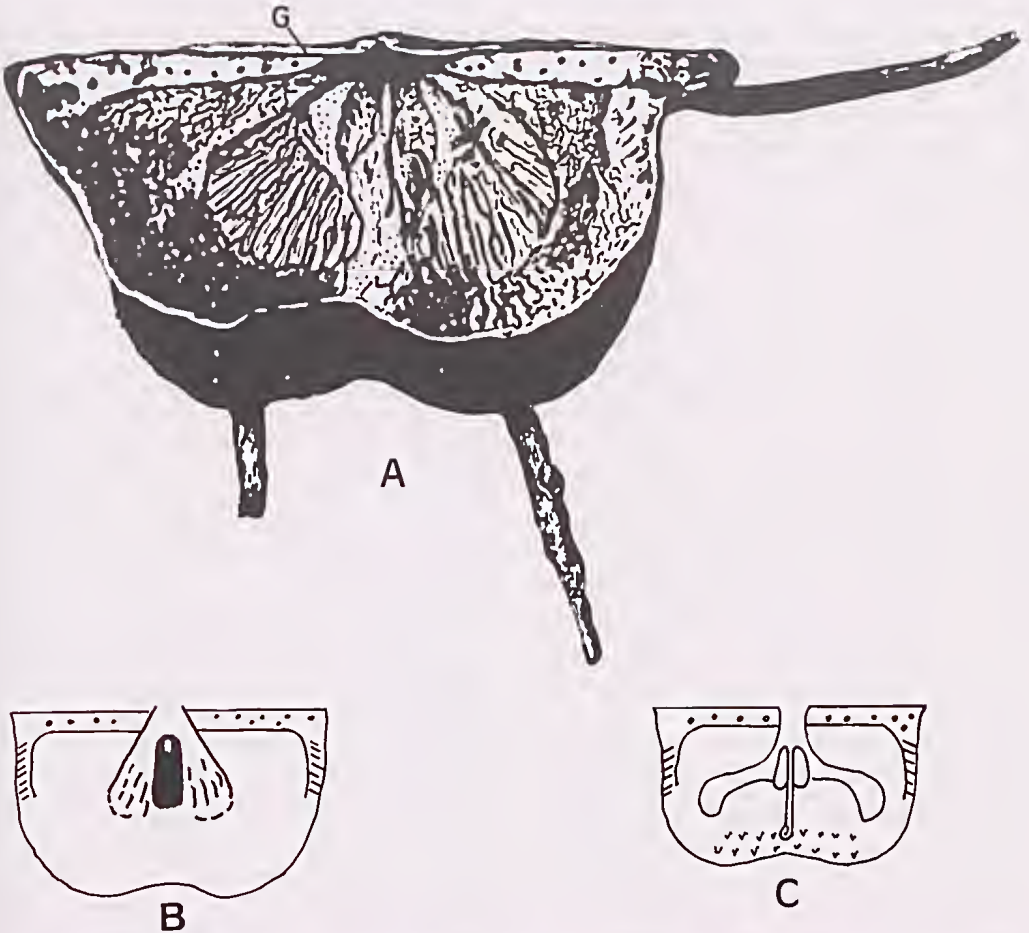


Fig. 1. A-C, Diagrams showing internal morphological characteristics of *Yakovlevia*. A, ventral interior of *Yakovlevia hessorum* Cooper & Grant (1975), redrawn from their pl. 473, fig. 1 to show the ginglymus (G), the rectangular transverse band below the ginglymus, and the ventral muscle field, $\times 2.1$; B, C, *Yakovlevia transversa* (Cooper) from northern Yukon Territory, Canada, showing ventral and dorsal interiors, respectively. (Fig. 1B drawn from a ventral internal mould and Fig. 1C from a latex cast of a dorsal internal mould, both $\times 1.2$ approximately.)

FAMILIAL POSITION OF *YAKOVLEVIA*

There have been varied opinions among brachiopod workers over the familial position of *Yakovlevia* (and *Muirwoodia*). Fredericks (1925) originally compared *Yakovlevia* with *Productus* Sowerby and placed the former in the Chonetinae Bronn. Likharev (1947) proposed *Muirwoodia* as a sub-genus of *Productus* but did not comment specifically on its familial/subfamilial position although the Productidae Gray may have been implied by him. This classification was also used by Kashirtsev (1959) and Sarycheva et al. (1960). More recent studies on *Yakovlevia* (and *Muirwoodia*) have demonstrated a broader range of potential familial positions for *Yakovlevia*. Muir-Wood & Cooper (1960) assigned *Yakovlevia* (and *Muirwoodia*) to their newly proposed subfamily Paucispiniferinae within the Linoproductidae Stehli. This grouping was based on the fact that both *Yakovlevia* (and *Muirwoodia*) and *Paucispinifera* are characterised by few (four or more) halteroid spines and a sessile, dorsally recurved, trilobate cardinal process. This classification was subsequently adopted by Muir-Wood (1965) and Barchatova (1970). However, Waterhouse & Piyasin (1970, p. 92) rejected this scheme, arguing that (1) the Paucispiniferinae 'is clearly Marginiferid', and (2) 'Genera associated with *Paucispinifera* by these authors (Muir-Wood & Cooper) such as *Yakovlevia* and *Muirwoodia* are not Marginiferid', but rather probably 'belong with the Linoproductidae'. This argument was later reinforced and formalised by Waterhouse (1975) by proposing the new subfamily Yakovleviinae within the Linoproductidae, in which he included three genera: *Yakovlevia*, *Muirwoodia* and *Duarteia* Mendes (1959). Waterhouse (1978) uplifted the Yakovleviinae to the family rank within the superfamily Linoproductacea. Independently, Cooper & Grant (1975) also separated *Yakovlevia* from the Paucispiniferidae and placed it in the Linoproductidae. Kalashnikov (1980), on the other hand, while recognising *Muirwoodia* assigned this genus to the Retariidae Muir-Wood & Cooper on the grounds that the dorsal interior of *Muirwoodia pseudoartiensis* (Stuckenberg) he described shows cardinal and lateral ridges and a diaphragm, resembling the dorsal interior of *Retaria* Muir-Wood & Cooper and allies. Kalashnikov's proposition was however not accepted by Abramov & Grigor'yeva (1983), who pointed out that the cardinal and lateral ridges and the diaphragm were not persistent features for all *Muirwoodia* species and certainly not present in *M. mammata* (Keyserling), the type species of the genus. These authors instead recognised the Yakovleviidae.

Another opinion regarding the familial assignment of *Yakovlevia* was expressed by Kalashnikov (in Meyen 1983), who linked the genus to the Anidanthidae Waterhouse, but no explanation was given. More recently, Lazarev (1990) also recognised the family Yakovleviidae but he placed it in the superfamily Productacea, arguing that (1) the early representative of the Yakovleviidae, *Sajakella* Nasikanova (in Grigor'yeva & Nasikanova 1968), has coarser costellae that resemble those of the Inflatidae Sarycheva, and (2) that there exists 'striking similarity' in dorsal internal structures between *Yakovlevia* and representatives of *Horridonia* Chao, although no specific comparisons were given.

In this paper, I also recognise the family Yakovleviidae but disagree with Lazarev on his classification of this family with the Productacea on three main grounds. Firstly, although *Sajakella formosa* Nasikanova (in Grigor'yeva & Nasikanova 1968), type species of *Sajakella*, has costellate appearance that indeed suggests similarity to *Inflatia* Muir-Wood & Cooper and allies, but *Inflatia* and related genera lack the four or more halteroid spines that characterise *Sajakella* and other yakovleviid genera and have usually much coarser costellae, a strongly convex visceral disc, a roundedly geniculated trail, and a prominent reticulation pattern on the visceral disc. To the contrary, I would argue that the fine capillate to costellate exterior of the Yakovleviidae alone clearly relate this group to the linoproductids. Secondly, although the transverse outline, flattened visceral disc, and the paucity of long, erect halteroid spines of *Yakovlevia* and allies appear to suggest some degree of resemblance to *Paucispinifera*, as noted initially by Muir-Wood & Cooper (1960), but the latter has strong marginal ridges and a cardinal process allied to that of *Marginifera* Waagen and *Kozlowskia* Fredericks, all with a distinct zygidium. In addition, *Yakovlevia* and *Paucispinifera* differ significantly in the distribution pattern of their halteroid spines; the former always has four basic halteroid spines: one on each ear and one on the trail on each side of the sulcus just anterior to the venter, as opposed to *Paucispinifera* which always has six large halteroid spines: one on each ear, one on each umbonal slope, and one on each side of the sulcus, as well as a row of additional smaller spines up the furrow demarcating ears (Muir-Wood & Cooper 1960, p. 320). Thirdly, Lazarev's observation that *Yakovlevia* has 'striking similarity' in dorsal internal structures to those of *Horridonia* is probably inadequate because the former usually has well-differentiated anterior and posterior adductor scars at maturity and a much lower

cardinal process with separated lobes typical of the linoproductids (see Muir-Wood & Cooper 1960: pl. 120, fig. 7; Cooper & Grant 1975: pl. 471, fig. 22) compared with the dorsal interior of *Horridonia*, which is characterised by non- or ill-differentiated adductor sears and a high cardinal process usually supported by a shaft (see Muir-Wood & Cooper 1960: pl. 108, fig. 8).

STRATIGRAPHICAL AND PALAEOGEOGRAPHICAL DISTRIBUTION OF *YAKOVLEVIA*

Forty-seven species have been recorded previously under the names of *Yakovlevia* and *Muirwoodia*, most of them having been described and illustrated. Of these, 45 are recognised in this paper in view of the definition of *Yakovlevia* adopted herein (Table 1, Fig. 2). The other two recorded forms that are excluded from this list are *Muirwoodia? aurita* Volgin (1960) from the Middle Carboniferous Uchbulak Horizon of Fergana and *Muirwoodia* sp. (Minato & Tazawa 1977) from the Lower or Middle Permian unnamed strata in

southern Chile. The first species probably belongs to *Protanidanthus* Liao (1979) for it has a strongly transverse and fusiform outline, a strong but rounded geniculation of the ventral valve, poorly demarcated ears, and coarse costellae. The Chilean species recorded by Minato & Tazawa is represented by three poorly preserved specimens; they are probably either a *Duartea* sp. or an *Anidanthus* sp. Very little was known about the ventral valve except for a large halteroid spine extruding from one ear, suggesting *Yakovlevia* or *Duartea*, but the dorsal valve was said to be covered with undulated rugae in addition to costellae, resembling the dorsal ornament of *Anidanthus* Whitehouse, or allies.

It is clear from Table 1 and Fig. 2 that *Yakovlevia* has both a restricted stratigraphical and geographical distribution. The genus first appeared in the Middle Carboniferous in the Urals and Russian Platform, probably evolved from *Sajakella* through *Productus martianovi* Lapina (1957), a species assigned tentatively to *Sajakella* by Nasikanova (in Grigor'yeva & Nasikanova 1968) but transferred to '*Muirwoodia*' by Kalashnikov (1980), due to its 'transitional' characteristics, especially in external

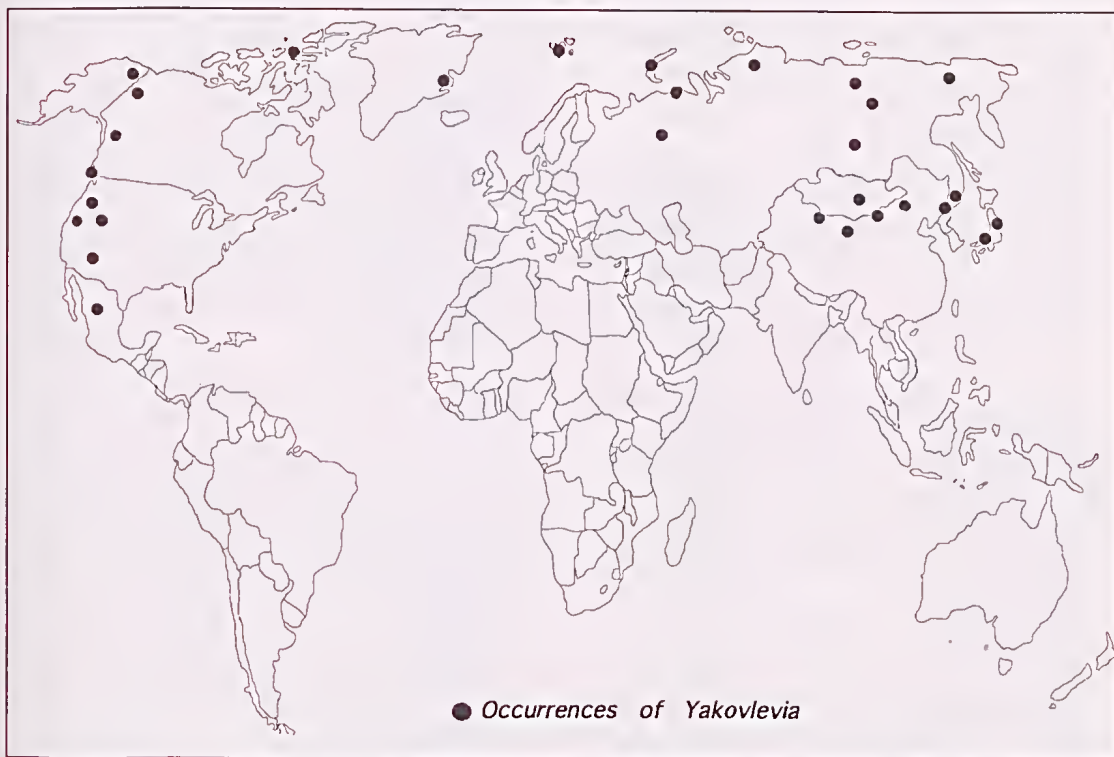


Fig. 2. Global occurrences of *Yakovlevia* species recognised in this paper.

Species	Geographic distribution	Age range	Key references
<i>Yakovlevia mammata</i> (Keyserling 1846)	The Urals, Novaya Zemlya, NE Siberia, Taimyr Peninsula, Spitsbergen, Mongolia, NE China, Canada, Alaska, Spitsbergen; Greenland	?Asselian to Kungurian	Chernyshev 1902; Kashirtsev 1959; Harker & Thorsteinsson 1960; Zavodovskiy & Stepanov 1971; Brabb & Grant 1971; Nakamura et al. 1992
<i>Yakovlevia multistriata</i> (Meek 1860)	Phosphoria and Park City Formations, Great Basin, U.S.A.	Wordian (?Kazanian)	Yochelson 1968
<i>Yakovlevia weyprechtii</i> (partim.) (Toula 1873)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian- Ufimian	Toula 1873; Wiman 1914; Dunbar 1955; Nakamura et al. 1992
<i>Yakovlevia impressa</i> (Toula 1875)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian- Ufimian	Toula 1875; Wiman 1914; Dunbar 1955; Nakamura et al. 1992
<i>Yakovlevia artiensis</i> (Chernyshev 1889)	The Urals and Russian Platform	U. Carboniferous to Artinskian	Chernyshev 1889; Kalashnikov 1980
<i>Yakovlevia pseudo- artiensis</i> (Stueckenberg 1905)	The Urals and Russian Platform	U. Carboniferous to Artinskian	Stueckenberg 1905; Kalashnikov 1980
<i>Yakovlevia geniculata</i> (Girty 1910)	Park City Formation, Idaho, U.S.A.	Wordian (?Kazanian)	Girty 1910
<i>Yakovlevia duplex</i> (Wiman 1914)	Kapp Starostin Formation and equivalents in Spitsbergen and Greenland	Kungurian- Ufimian	Wiman 1914; Dunbar 1955; Nakamura et al. 1992
<i>Yakovlevia kaluzinensis</i> Fredericks 1925	Chandlaz Suite, Sikhote Alin, Russia	Kungurian- Ufimian	Fredericks 1925; Likharev & Kotlyar 1978
<i>Yakovlevia mannmati- formis</i> (Fredericks 1926)	The Urals and NE Siberia, Mongolia and north China	Sakmarian- Artinskian	Fredericks 1926; Ustritskiy 1971
<i>Yakovlevia svalbardensis</i> Frebald 1937	Spitsbergen	Kungurian- Ufimian	Frebald 1937
<i>Yakovlevia deminutivus</i> (Cloud 1940)	Mexico	Early Permian	Cloud 1944
<i>Yakovlevia</i> sp.	Monos Formation, Mexico	Wordian (?Kazanian)	Cooper in Cooper et al. 1953
<i>Yakovlevia greenlandica</i> (Dunbar 1955)	Kapp Starostin Formation or equivalents, Spitsbergen and Greenland	Kungurian to Ufimian	Dunbar 1955; Gobbett 1964; Nakamura et al. 1992
<i>Yakovlevia transversa</i> (Cooper 1957)	Coyote Butte Formation, central Oregon; Jungle Creek Fm., Yukon Territory; Vancouver Island	Sakmarian to ?Kungurian	Cooper 1957; this paper
<i>Yakovlevia californica</i> (Coogan 1960)	Nosoni Formation, northern California	?Kungurian	Coogan 1960
<i>Yakovlevia tinanica</i> Barchatova 1970	Timan Range, Russia	Kungurian	Barchatova 1970
<i>Yakovlevia parainpressa</i> Barchatova 1970	Timan Range, Russia	Kungurian	Barchatova 1970
<i>Yakovlevia anterospinosa</i> Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian- Ufimian)	Cooper & Grant 1975
<i>Yakovlevia sulcata</i> Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian- Ufimian)	Cooper & Grant 1975
<i>Yakovlevia costellata</i> Cooper and Grant 1975	Cherry Canyon Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975

Table 1. Stratigraphic and geographic distribution of *Yakovlevia* (= *Muirwoodia*) species.

Species	Geographic distribution	Age range	Key references
<i>Yakovlevia immatura</i> Cooper and Grant 1975	Road Canyon Fm., Texas	Roadian (Kungurian- Ufimian)	Cooper & Grant 1975
<i>Yakovlevia hessorum</i> Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
<i>Yakovlevia indentata</i> Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
<i>Yakovlevia intermedia</i> Cooper and Grant 1975	Word Fm., Texas	Wordian (?Kazanian)	Cooper & Grant 1975
<i>Yakovlevia mucronata</i> (Lee and Gu 1976)	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia baerginensis</i> Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia unisnuata</i> Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia ambigua</i> Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia penusa</i> Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia baiyinensis</i> Lee and Gu 1976	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu 1976
<i>Yakovlevia paramammata</i> Lee and Gu 1980	Sijjashan Fm., Helongjiang Prov., NE China	Artinskian- Kungurian	Li & Gu 1980
<i>Yakovlevia complanata</i> Lee and Gu 1980	Wujiatong Fm., Helongjiang Prov., NE China	Artinskian- Kungurian	Li & Gu 1980
<i>Yakovlevia paragreenlandica</i> Lee and Gu 1980	Dashisai Fm., Helongjiang Prov., NE China	Artinskian- Kungurian	Li et al. 1980
<i>Yakovlevia taxiensis</i> Lee and Gu 1980	Tumenling Fm., Helongjiang Prov., NE China	Artinskian- Kungurian	Li et al. 1980
<i>Yakovlevia dimorpha</i> Lee and Gu 1980	Dashisai, Helongjiang Prov., NE China	Artinskian- Kungurian	Li et al. 1980
<i>Yakovlevia sinuata</i> Lee and Gu 1980	Wujiatong Fm., Helongjiang Prov., NE China	Artinskian- Kungurian	Li et al. 1980
<i>Yakovlevia yujiagouensis</i> (Lee and Gu 1980)	Lower Permian, Helongjiang Prov., NE China	Artinskian- Kungurian	Li et al. 1980
<i>Yakovlevia martianovi</i> (Lapina 1957)	The Urals and Russian Platform	M. Carboniferous- Early Permian	Kalashnikov 1980
<i>Yakovlevia usualis</i> (Duan and Lee 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu in Ding et al. 1985
<i>Yakovlevia spinosa</i> (Duan and Lee 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Li & Gu in Ding et al. 1985
<i>Yakovlevia borealis</i> (Liu and Waterhouse 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Liu & Waterhouse 1985
<i>Yakovlevia convexus</i> (Liu and Waterhouse 1985)	Zhesi Fm., Inner Mongolia, NE China	Artinskian- Kungurian	Liu & Waterhouse 1985
<i>Yakovlevia</i> sp.	Honshu Island, Japan	Kungurian	Horikoshi et al. 1987
<i>Yakovlevia</i> sp.	Kitakami Mountains, Japan	Middle Permian	Tazawa 1987

Table 1 (continued).

ornament, between the two genera. This species is, in particular, characterised by costellae that are coarser than those found in typical *Yakovlevia* but finer than those seen in *Sajakella formosa* Nasikanova (in Grigor'yeva & Nasikanova 1968), the type species of *Sajakella*. Apart from *Yakovlevia martianovi*, only two other species are known from the Upper Carboniferous, *Y. artiensis* (Chernyshev 1889) and *Y. pseudoartiensis* (Stuckenber 1905), both persisting into the Lower Permian and confined to the Urals and the Russian Platform (Table 1).

Yakovlevia diversified in the Early Permian (two-fold Permian System), especially in the Late Artinskian to Kungurian times when it spread across the Boreal Realm as well as penetrating into the western coast of North America, Central America (Mexico), north and northeast China, Sikhote Alin, and central and northeast Japan (Fig. 2). In northeast China, Sikhote Alin, and Japan, *Yakovlevia* species of this age are found in association with not only other typical Boreal elements such as *Sowerbina* Fredericks, *Timaniella* Barchatova, and *Tunarinia* Solomina & Grigor'yeva, but also typical warm-water Tethyan genera including *Tylopecta* Muir-Wood & Cooper, *Compressoproductus* Sarycheva, *Spino-*

marginifera Huang, and *Permundaria* Nakamura, Kato & Choi (Tazawa 1991; Shi & Archbold 1995). This peculiar mixed-type fauna is very characteristic for the mid-Permian (Late Artinskian to Kungurian/Ufimian) of the north China–Japan–Sikhote Alin region, or the Inner Mongolia–Japanese Transitional Zone (Tazawa 1991). However, the origin of this mixed or transitional (i.e. transitional between the Boreal and Tethyan Realms) fauna remains unclear although we have elsewhere (Shi et al. 1995) suggested that it may have been formed in an intracratonic seaway on a newly formed stationary margin of the North China Block as a consequence of faunal migration from both the Cathaysian Province of the Tethyan Realm in the south and the Verkolyman Province of the Boreal Realm in the north (Fig. 3).

Similarly, the juxtaposed occurrences of *Yakovlevia* in both the Cordilleran Province (Yancey 1975), the McCloud Belt or Province (Miller 1987; = 'Exotic Province' of Yancey 1975), and the Grandian Province (Yancey 1975) of western North America (Fig. 3) is also puzzling. According to Yancey (1975) and Stevens (1985), both the Cordilleran and Grandian provinces were situated on the stable North American craton during the Permian and their palaeobiogeographical

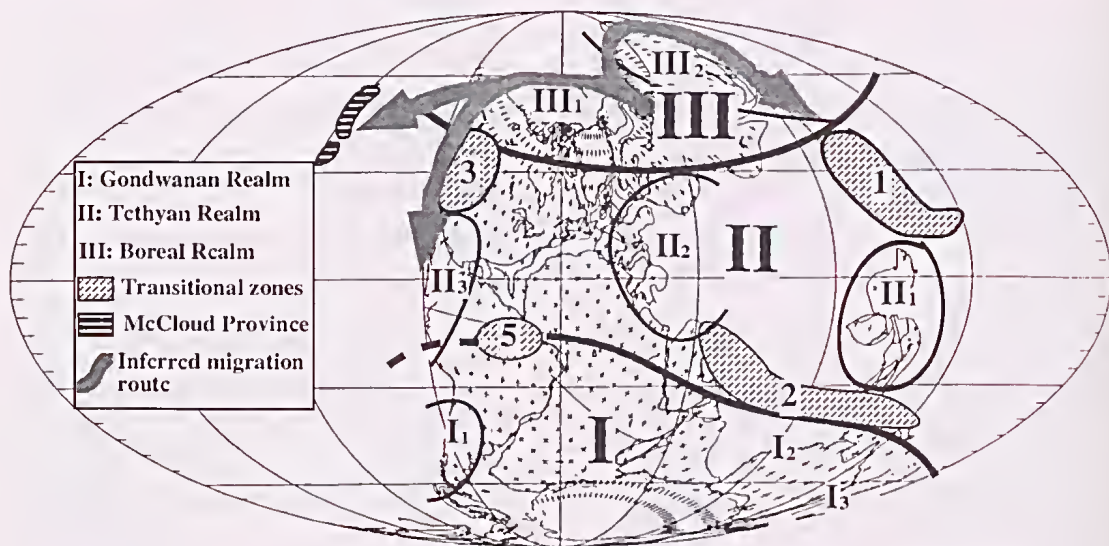


Fig. 3. Permian biogeographical realms and provinces and possible migration route of *Yakovlevia* during the Permian, modified from Shi et al. (1995) with the base map adopted from Scotese & MeckCrow (1990). The Permian biotic provinces are as follows: 1 = Northern Transitional Zone (Sino-Mongolian Province); 2 = Southern Transitional Zone (Cimmerian Province); 3 = Cordilleran Province; 1₁ = Paratitan Province, 1₂ = Westralian Province, 1₃ = Australasian Province; II₁ = Cathaysian Province, II₂ = West Tethys Province, II₃ = Grandian Province; III₁ = West Arctic Province; III₂ = Verkolyman Province.

differentiation may have resulted from the palaeo-latitude-related temperature differences. Thus, the occurrences of *Yakovlevia* in these two provinces may be explained using the scenario proposed by Ustritskiy (1968). He suggested that during the Late Carboniferous to Early Permian there were broad connections between the Arctic sea and the Tethys, one of which may have been via eastern Alaska–Yukon southward along the western margin of the North American craton to south-western United States–Central America. It was probably through this seaway connection that some typical Boreal elements including *Yakovlevia* migrated southwards into both the Cordilleran and Grandian provinces (Fig. 3).

However, the same scenario cannot be invoked to account for the presence of *Yakovlevia* in the McCloud Province (including such suspect terranes as Wrangellia, Grindstone and Eastern Klamath) because this province is now thought by many to have originated offshore and was separated from the North American craton by thousands of kilometres during the Permian (e.g. Stevens 1985; Stanley & Yancey 1990). This province contains a remarkable admixture of Boreal, Grandian, as well as Asian Tethyan faunal elements. The Asian Tethyan and Grandian components have been well recognised by previous studies (e.g. Stevens et al. 1990), presumably because of their abundance. However, the Boreal component has been largely overlooked. Among this category we may note the following brachiopod genera that have been described from central Oregon (Cooper 1957) and northern California (Coogan 1960): *Thule-productus* Sarycheva & Waterhouse, *Sowerbina* Fredericks, *Yakovlevia* Fredericks, *Septacamera* Stepanov, *Camerisma* (*Callaiapsida*) Grant, and *Spiriferella* Chernyshev. The origin of the McCloud Province has seen much recent debate and most workers now seem to agree that it represents a remnant of a Permian volcanic arc then located somewhere in the palaeo-Pacific, perhaps near the palaeo-Equator, with geographical proximities to both East Asia and North America (these proximities were necessary to account for the presence of both Asian Tethyan and Grandian elements) (e.g. Miller 1987; Stevens et al. 1990). Although this hypothesis appears to be supported by limited palaeomagnetic data (Mankinen et al. 1989) which indicate that the Eastern Klamath terrane was located at $17.8^{\circ} \pm 8.4^{\circ}N$ latitude, the presence of the Boreal elements in the province is hardly explainable using this scenario. To account for the importance of the Boreal elements, an alternative explanation is required. Therefore, I suggest that it is probably more likely that the

Eastern Klamath terrane and other terranes of the McCloud Province that contain both Boreal, Asian Tethyan and Grandian Permian faunas have originated in a more northerly position, perhaps in the palaeotemperate zone between palaeolatitudes 30° and $50^{\circ}N$, with geographical proximities to both East Asia, northeast Asia, and North America (Fig. 3).

YAKOVLEVIA TRANSVERSA ZONE FROM NORTHERN YUKON TERRITORY, WESTERN CANADA, AND ITS DISTRIBUTION IN NORTH AMERICA AND THE ARCTIC REGION

Fossils are abundant throughout the Permian marine sequences of the northern Yukon Territory, located in the Foreland Belt of western Canada (Fig. 4). Permian stratigraphy of this region was established by Bamber & Waterhouse (1971) and recently reviewed by Bamber et al. (1989). The marine Permian System comprises the Jungle Creek Formation in the lower part and the Tahkandit Formation in the upper, ranging in age from the Asselian to Wordian. Waterhouse (in Bamber & Waterhouse 1971) constructed a comprehensive biozonation scheme for the entire Permian succession based on brachiopod faunas, most of which are yet to be described. He proposed some 6 biozones for the Jungle Creek Formation and 4 for the overlying Tahkandit Formation. These zones were considered to be assemblage biozones. I (Shi 1994) have recently described the *Jakuto-productus verchoyanicus* Zone (formerly known as the *Jakuto-productus* Zone), of the Early Artinskian (Aktastinian) age, from the top of the Jungle Creek Formation. The present paper provides a review of another zone, the *Yakovlevia transversa* Zone [i.e. the *Yakovlevia* Zone (or Ey zone) of Waterhouse in Bamber & Waterhouse 1971] from the lower-middle part of the Jungle Creek Formation.

In northern Yukon territory, the *Yakovlevia transversa* Zone occurs above the *Tomioopsis-Attenuatella* Zone and below either the '*Attenuatella*' Zone (the so-called '*Attenuatella*' is yet to be renamed as a new genus) or the *Tornquistia* Zone, and is distinguished overall by the predominant occurrence of *Yakovlevia transversa* (Cooper) and absence of *Attenuatella* spp. that characterise the underlying *Tomioopsis-Attenuatella* Zone. The fauna of the *Yakovlevia transversa* Zone is large, comprising 57 of the 67 brachiopod species I (Shi 1991) described from the middle and upper parts of the Jungle Creek Formation, dominated by productids and to less extent by spiriferids.

Of the total 57 brachiopod species present in this zone, 20 are restricted to it, at least 8 were also found in the underlying *Tomioopsis-Attenuatella* Zone according to data in Waterhouse (in Bamber & Waterhouse 1971), and 28 range into overlying zones. In terms of abundance, short range, and wide distribution, the diagnostic elements of this zone include the following species: *Arctitreta* n. sp., *Komiella omolonensis* (Likharev), *Fimbrinia* n. sp., *Tubersulculus maximus* Waterhouse, *Kutorginella yukonensis* Sarycheva & Waterhouse, *Rugivestis* n. sp., *Waagenoconcha permocarbonica* Ustritskiy, *Calliprotonia inexpecta* (Cooper), *Reticulatia*

uralica (Chernyshev), *Antiquatonia cooperi* Shi, *Linoproductus dorotheevi* Fredericks, *Protoandanthus* n. sp., *Yakovlevia transversa* (Cooper), *Rhynchopora magna* Cooper, *Spiriferella pseudodraschei* Einor, Syringothyrid? n. gen. et sp., *Domokhotia* n. sp., *Spirelytha fredericksi* Archbold & Thomas, and a bivalve *Acanthopecten licharewi* (Fredericks). Of these characteristic constituents, the nominal species, *Yakovlevia transversa*, is most widespread and abundant, as well as very diagnostic in morphology, and thus may be easily recognized in the field. This species is not restricted to this zone, however; it has also been found

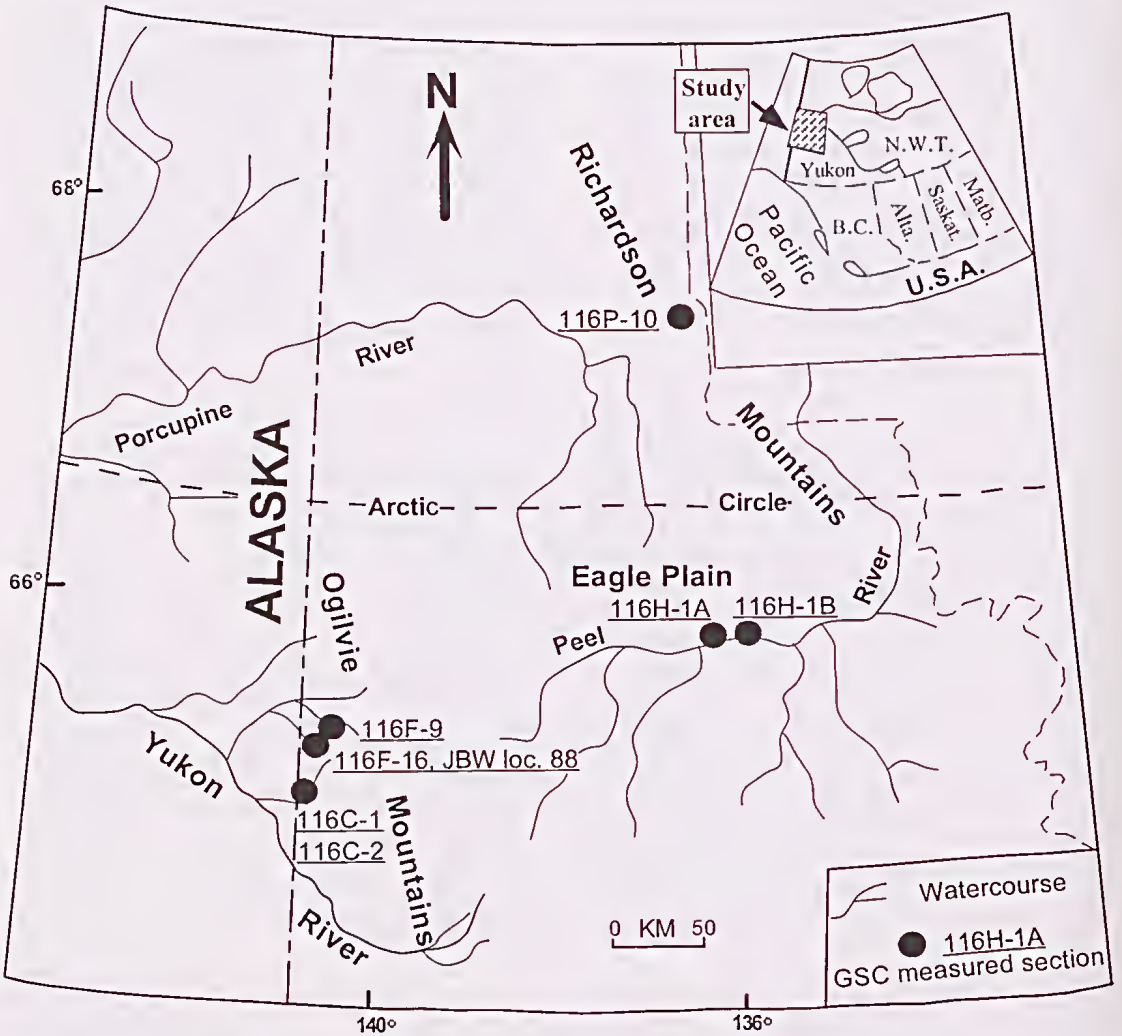


Fig. 4. Map showing area of study and the location of Geological Survey of Canada (GSC) sections referred to in the text and where the *Yakovlevia transversa* Zone has been recorded.

sporadically in the overlying 'Attenuatella' and *Jakutoproductus verchoyanicus* zones (Shi 1991, 1994).

The base of the *Yakovlevia transversa* Zone is defined by the disappearance of species of *Attenuatella* and the first appearance of such species as *Arctitreta* n. sp., *Rugivestis* n. sp., *Protoanidanthus* n. sp., *Spirelytha fredericksi*, and the co-occurrence of abundant *Fimbrinia* n. sp., *Kutorginella yukonensis*, *Yakovlevia transversa*, and *Rhynchopora magna*. The upper boundary approximately corresponds to the lower limit of the overlying 'Attenuatella' Zone, which is marked by the restricted and abundant occurrence of this new ambicoeliid species; or the *Tornquistia* Zone characterised by *Tornquistia* sp. and a distinct ammonoid fauna described by Nassichuk (1971).

The reference section of the *Yakovlevia transversa* Zone is designated at GSC section 116H-1A

along the Peel River, southern Eagle Plain (Figs 4 and 5). The lithostratigraphy of this section has been fully described by Bamber (1972). In this section, the *Yakovlevia transversa* Zone occurs from approximately 24 m to 210 m above the base of the Jungle Creek Formation and is identified by more than 20 species (see Fig. 5), notably *Komiella omolonensis* (Likharev), *Waagenoconcha permocarbonica*, *Kutorginella yukonensis*, *Kochiproductus porrectus* (Kutorga), *Yakovlevia transversa*, *Camerisma (Callaiapsida) pentameroides* (Chernyshev), *Spiriferella saranae* (Verneuil), *Alispiriferella ordinaria* (Einor), *Tomiopsis ovulum* Waterhouse, and *Dielasma brevicostatum* Cooper.

The *Yakovlevia transversa* Zone appears to be widely distributed in the northern Yukon Territory. In addition to the reference section, this zone has also been recorded from the GSC sections 116F-9, 116F-16, 116C-1, and 116C-2 in the northern

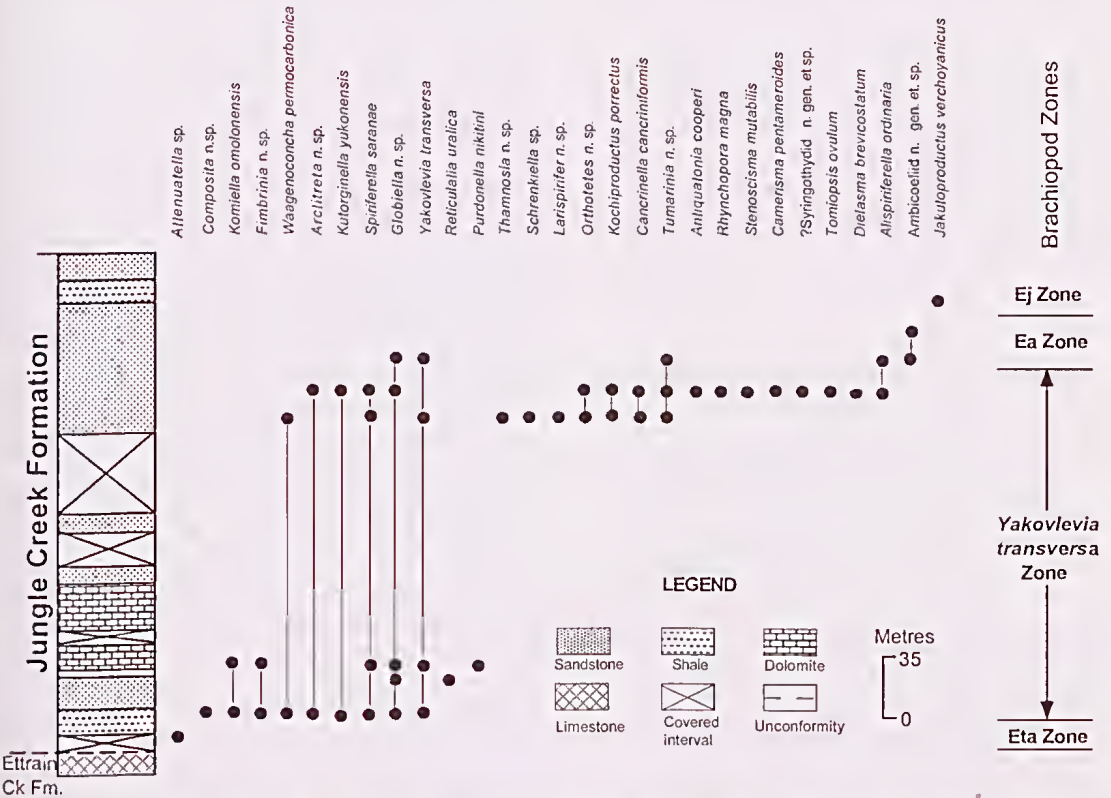


Fig. 5. Reference section of the *Yakovlevia transversa* Zone (GSC section 116H-1A), Peel River, southern Eagle Plain, northern Yukon Territory. The succession of the brachiopod zones as proposed by Waterhouse (in Bamber & Waterhouse 1971) are as follows: Eta Zone—*Tomiopsis-Attenuatella* Zone; Ea Zone—'Attenuatella' Zone (the so-called 'Attenuatella' is yet to be renamed as a new genus); Ej Zone—*Jakutoproductus verchoyanicus* Zone (this zone has been fully described recently by Shi 1994).

Ogilvie Mountains, section 116H-1B on the Peel River of southern Eagle Plain, and in the section 116P-10, northern Richardson Mountains (Fig. 4).

Overall, the brachiopods of the *Yakovlevia transversa* Zone appear to indicate a general Sakmarian age, most likely Early Sakmarian (Tastubian) in view of both brachiopods and an ammonoid species found in the same zone. Many species characteristic for this zone are also common in the Sakmarian Stage of the Urals, as summarized by Miloradovich (1949), Stepanov (1951), and Kalashnikov (1986), notably *Reticulatia uralica*, *Tubersulculus maximus* (probably conspecific with *Productus pseudocucleatus* Krotov of Chernyshev 1902), *Kochiproductus porrectus*, *K. saranaeanus* Fredericks, *Linoproductus dorotheevi* [= *Linoproductus cora* (not d'Orbigny) of Chernyshev and also comparable with *L. rhiphaeus* Stepanov), *Cancrinella cancriniformis* (Chernyshev), and *Purdonella nikitini* (Chernyshev). Of these species, *Linoproductus rhiphaeus* was cited to be confined to the Tastubian in the Urals (Kalashnikov 1986, p. 90), and *Reticulatia uralica* and *Tubersulculus maximus* first appeared in the Tastubian in the Urals (Stepanov 1951, p. 104). *Yakovlevia transversa* is very close to *Y. mammatiformis* (Fredericks), a species that Kalashnikov (1986) figured as one of the leading forms of the Sakmarian Stage in the Urals. *Y. mammatiformis* is also characteristic for the Sezim Suite of the Pechora Basin, north Urals (Ifanova 1972; Kalashnikov in Meyen 1983), which has been well dated Late Asselian to Sakmarian by ammonoids (Andrianov 1985).

Two taxa of the *Yakovlevia transversa* Zone are identical to or closely resemble species from the Southern Hemisphere and also support a general Sakmarian age for this zone. *Globiella* n. sp. is similar to *Globiella umariensis* (Reed) from the Umaria Beds of Peninsular India, of Early Sakmarian (Tastubian) age (Archbold 1983). The second species, *Spirelytha fredericksi* Archbold & Thomas, is confined to the *Yakovlevia transversa* Zone in northern Yukon Territory. The same species is elsewhere known only from the Late Sakmarian (Sterlitamakian) fauna of the Callytharra Formation in Western Australia (Archbold & Thomas 1984).

The ammonoid species, *Tabantalites bifurcatus* Ruzhencev (1952), was reported by myself (Shi 1991) from GSC loc. 57053 (assigned to the *Yakovlevia transversa* Zone) in the section 116F-16 in the northern Ogilvie Mountains. In south Urals, *T. bifurcatus* is known only from the upper Asselian and lower Sakmarian (Tastubian) strata (Ruzhencev 1952).

Thus, by judging from both brachiopods and the ammonoid summarized above, it seems most likely that the *Yakovlevia transversa* Zone is of Early Sakmarian (Tastubian) age. This age assignment would be consistent with the Late Asselian age of the underlying *Tomioopsis-Attenuatella* Zone proposed by Waterhouse & Waddington (1982).

Beyond the Yukon Territory, the *Yakovlevia transversa* Zone is found to be correlative with a few Permian faunas in western North America and the Arctic. Logan & McGugan (1968) listed and partially described a brachiopod fauna from the Telford Formation in southeastern British Columbia, including the following identifiable species: *Kutorginella* sp. cf. *K. neoinflatus* (Likharev), *Anidanthus eucharis* (Girty), *Yakovlevia* sp. cf. *Y. greenlandica* Dunbar (probably *Y. transversa*), *Spiriferella saranae*, and *Alispiriferella* sp. cf. *A. ordinaria*, *Purdonella* sp. cf. *P. nikitini*, and 'Spirifer' *osborni* Harker. As a whole, this assemblage appears to suggest a generalized, perhaps condensed or latitudinally differentiated, correlation with faunas from the Yukon Jungle Creek Formation, more likely the *Yakovlevia transversa* Zone. A more positive correlation may be made between the Yukon *Yakovlevia transversa* Zone with the fauna from the Lower Permian 'Formation B' in the Butte Lake area of Vancouver Island (Yalc 1963). Of some 15 brachiopod species found from this unit, 9 are shared by the Yukon *Yakovlevia transversa* Zone, including species characteristic of this zone such as *Calliprotonia inexpecta*, *Kochiproductus porrectus*, *Antiquatonia cooperi*, *Sowerbina bullocki* (Nelson & Johnson), *Yakovlevia transversa*, *Neospirifer* sp., *Rhynchopora magna*, *Spiriferella saranae*, and *Camerisma (Callaiapsida) pentameroides*.

There seems to exist a great similarity of the Yukon Jungle Creek brachiopod faunules to brachiopods from the upper part of the Coyote Butte Formation in central Oregon, northwestern United States, described by Cooper (1957). Cooper considered the Oregon brachiopod fauna most likely to be Roadian or Kungurian in age, a conclusion that seems to be also in agreement with the age determination from fusulinids and sparse conodonts found from the same formation (Wardlaw et al. 1982). However, this age is inconsistent with the Asselian to Early Artinskian age assigned to the Yukon Jungle Creek faunules. There are no single species found in common between the Roadian brachiopod fauna of West Texas and the Coyote Butte fauna. On the other hand, there are ten species from the Oregon fauna that have also been found in the Yukon Jungle Creek faunules, of which nine are known from the *Yakovlevia*

transversa Zone: *Krotovia pustulata* (Keyserling); *Calliprotonia inexpecta*, *Kochiproductus porrectus*; *Waagenoconcha parvispinosa* Cooper, *Antiquatonia cooperi*, *Linoproductus dorotheevi*; *Yakovlevia transversa*, *Rhynchopora magna*, and *Spiriferella pseudodraschei*. Clearly, there is a need to reassess the biostratigraphical and palaeobiogeographical implications of the Oregon brachiopod fauna in the light of modern taxonomy and recent advances on the geology of surrounding areas, in order to resolve the discrepancy on the age determination and correlation of the Oregon fauna.

The *Yakovlevia transversa* Zone is also traceable at many Arctic localities but detailed correlation with these Arctic assemblages is hindered by the lack of modern revisions of the Arctic faunas. A large Permian brachiopod fauna was described by Likharev & Einor (1939) from a number of localities on Novaya Zemlya. The majority of species described were collected from the Barents Series on the western coast of the north island, between Sedov Bay and Russian Harbour. This fauna consisted of some 63 species, of which 5 are also found in the Yukon *Yakovlevia transversa* Zone: *Orthotichia morganiana* (Derby), *Kochiproductus saranaeanus*, *Reticulatia uralica*, *Spiriferella pseudodraschei*, and *S. saranae*. In addition, a few more species may be compared with representatives from the Yukon zone, including *Calliprotonia sterlitamakensis* Stepanov (close to Yukon *C. inexpecta*), *Schrenkiella schrenki* (Stuckenbergl) (similar to Yukon *Schrenkiella* sp.), and *Rhynchopora nikitini* (Chernyshev) (comparable with Yukon *R. magna*). On the other hand, the Barents Series also contains *Thuleproductus arcticus* (Whitfield) and *Anemonaria pseudohorrida* (Wiman), which normally occur in younger Permian (Kungurian or younger) deposits in the Arctic region. Thus, the Barents Series may have a longer age range than the Yukon *Yakovlevia transversa* Zone; or the listed fauna of the Barents Series may have been mixed from two or more assemblages of different age.

Permian brachiopods of the Taimyr Peninsula were described by Einor (1939, 1946) and Ustritskiy & Chernyak (1963). The fauna from the upper Turuzov Horizon, assigned an Asslian to Sakmarian age by Ustritskiy & Chernyak (1963), appears to be at least in part correlative with the Yukon *Yakovlevia transversa* Zone. Species common to both areas are *Dyoros (Dyoros) pseudotrapezoidalis* (Miloradovich), *Fimbrinia* n. sp., and *Waagenoconcha permocarbonica*.

The brachiopod fauna from the Afonin Horizon of the Verchoyan Mountains in northeast Siberia, described by Kashirtsev (1959) and Abramov &

Grigor'yeva (1988), appears to be in part correlated with the Yukon *Yakovlevia transversa* Zone, with the following species in common or closely comparable: *Anidanthus? sarytchevae* Zavodovskiy (close to Yukon *Protoanidanthus* n. sp.), *Fimbrinia* n. sp., *Kochiproductus porrectus*, '*Marginifera? peregrina* (not Fredricks) (in part conspecific with Yukon *Rugivestis* n. sp.), and *Canocrinella cancriniformis* (Chernyshev). A similar fauna has also been reported from the Irbichan Horizon of the Kolyma-Omolon Massif in northeast Siberia (Zavodovskiy & Stepanov 1971), with the following species shared with or closely related to those of the Yukon *Yakovlevia transversa* Zone: *Overtonia gijigensis* Zavodovskiy (close to Yukon *Fimbrinia* n. sp.), *Canocrinella cancriniformis*, *Anidanthus aagardi* (not Toulal) (close to Yukon *Protoanidanthus* n. sp.), *Yakovlevia mammatifornis* (close to Yukon *Y. transversa*), *Kitakamithyris stepanovi* (Zavodovskiy) (comparable with Yukon *Spirelythia* sp.).

The *Yakovlevia transversa* Zone can be traced further north in Spitsbergen, where correlative faunas occur in the upper Wordiekammen Limestone (see Gobbett 1964) in central Vestspitsbergen and in the Treskelodden Beds on the northeastern coast of Hornsund, southwestern Vestspitsbergen (Czarnecki 1969). With both Spitsbergen assemblages the Yukon zone shares *Reticulatia uralica* (Chernyshev), *Linoproductus dorotheevi* (Fredericks), and *Canocrinella singletoni* Gobbett.

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Superfamily LINOPRODUCTACEA Stehli, 1954 (nom. transl. Waterhouse, 1978; ex. LINOPRODUCTIDAE Stehli, 1954)

Family YAKOVLEVIIDAE Waterhouse, 1975 (nom. transl. Waterhouse, 1978; ex. YAKOVLEVIINAE Waterhouse, 1975)

Diagnosis. Subquadrate to transverse shells with wide hinge margin and well demarcated ears and abrupt geniculation; visceral disc flattened to gently concavo-convex; shell surface capillate to costellate; ventral valve normally with 4 basic, large halteroid spines: one on each ear and one on each side of sulcus just anterior to the venter, and rare, scattered body spines; no dorsal spines. Marginal ridges absent to very weakly developed.

Genera included and discussion. The following genera are included in the family: *Sajakella* Nasi-

kanova (in Sarycheva et al. 1968), *Yakovlevia* Fredericks (1925), *Duarte* Mendes (1959), and ?*Paramuirwoodia* Zhang (in Zhang et al. 1983). Inclusion and the validity of *Paramuirwoodia* is questionable. This genus, with type species *P. quadrata* Zhang (in Zhang et al. 1983), is characterised by a subquadrate to slightly transverse outline, abrupt geniculation, costellate shell surface, and a pair of large halteroid spines on umbonal slopes of the ventral valve. Apart from the spine pattern, all other characteristics of this genus can be closely compared with those of *Productus batesianus* Derby (1874), the type species of *Duarte* (note that *Duarte* has 4 large halteroid spines, like *Yakovlevia*). In addition, both type species also have weakly developed marginal ridges in the dorsal valve (see Zhang in Zhang et al. 1983: pl. 133, fig. 1d; Mendes 1961: fig. 16). Although Zhang defined *Paramuirwoodia* as possessing only one pair of halteroid spines on umbonal slopes of the ventral valve (this pattern is unlike any other yakovleviid genus), at least one additional large halteroid spine base is clearly shown on one side of the ventral trail next to the sulcus in *Paramuirwoodia quadrata* (see Zhang in Zhang et al. 1983: pl. 133, fig. 1a). If this observation is correct, the overall spine pattern of *Paramuirwoodia* seems more like that of *Paucispinifera* than that of *Yakovlevia*; however, the exact nature of the halteroid spines of *Paramuirwoodia* remains to be clarified, preventing any positive determination at the present as to its familial status and relationship with *Duarte*.

The combination of spine pattern, capillate to costellate exterior, flat to gently concavo-convex visceral disc, and the abruptly geniculated trail make the family Yakovleviidae unique within the Linoproductacea. No other linoproductaceans seem to have the four basic large halteroid spines symmetrically distributed on the ventral valves.

Genus *Yakovlevia* Fredericks, 1925

Yakovlevia Fredericks 1925: 7.—Muir-Wood & Cooper

1960: 323.—Sarycheva et al. 1960: 233.—Kotlyar 1961: 459.—Muir-Wood 1965: H506.—Grant in Brabb & Grant 1971: 16.—Cooper & Grant 1975: 1177.—Lazarev 1990: 85.

Muirwoodia Likharev 1947: 187.—Dunbar 1955: 111.—Muir-Wood & Cooper 1960: 322.—Muir-Wood 1965: H506.—Lazarev 1990: 85.

Diagnosis. Medium to large transverse Yakovleviidae, shell surface capillate to finely costellate, usually with a row of spines along hinge margin of ventral valve; marginal ridges absent to weakly developed.

Discussion. *Yakovlevia* is similar to *Sajakella* and *Duarte* in having the 4 basic large halteroid spines on the ventral valve, lack of dorsal spines, and an abrupt geniculation, but the latter two usually have notably coarser costellae. In addition, *Sajakella* seems to have relatively more finer body spines scattered on the ventral valve, and *Duarte* lacks a hinge row of spines according to Muir-Wood (1965) and is usually more quadrate than transverse in outline, and its ears are also less demarcated. *Paramuirwoodia*, subjected to the clarification of its halteroid spines on the ventral valve, can be distinguished from *Yakovlevia* also by its coarser costellae, more quadrate outline, and the lack of a row of hinge spines.

Geographic distribution. Arctic, western North America, Mexico, north and northeast China, Japan, and eastern Russia (see Table 1, Fig. 2).

Stratigraphic distribution. Middle Carboniferous to Kazanian (see Table 1).

Yakovlevia transversa (Cooper, 1957)

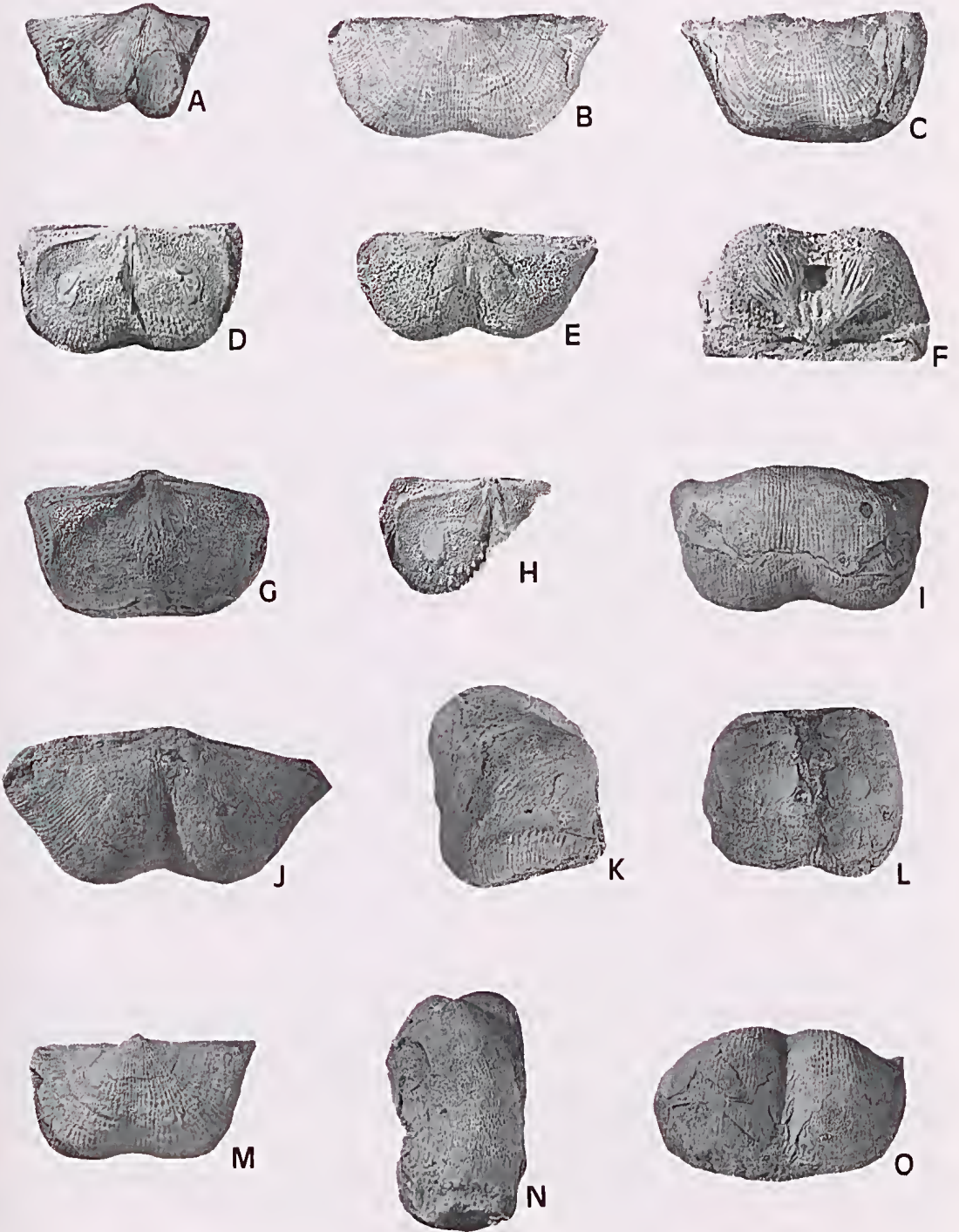
Fig. 6A–O

Muirwoodia transversa Cooper 1957: 39, pl. 5A, figs 1–13.

Yakovlevia sp. Waterhouse in Bamber & Waterhouse 1971: pl. 14, figs 2–5; pl. 15, fig. 1; pl. 16, fig. 7.

Yakovlevia transversa.—Nelson & Nelson (partim.) 1985: pl. 1, figs 10–11; not fig. 12.

Fig. 6. A–O, *Yakovlevia transversa* (Cooper, 1957). A, posterior view of ventral valve, GSC 97153 from GSC loc. 53946, GSC section 116C-1. B, 1, posterior and anterior views of ventral valve, GSC 97045 from GSC loc. 53721, section 116H-1B. C, posterior view of dorsal external mould, GSC 97148 from GSC loc. 53703, section 116H-1A. D, latex cast of dorsal internal mould, GSC 97052 from JBW loc. 88. E, ventral internal mould, GSC 97152 from JBW loc. 88. F–G, ventral internal mould and latex cast, GSC 97051 from JBW loc. 88. H, latex cast of dorsal internal mould, GSC 97055, JBW loc. 88. J, posterior view of ventral valve, GSC 97046 from GSC loc. 56972, section 116F-16. K, lateral view of ventral internal mould, GSC 97053 from GSC loc. 53860, section 116P-10. L, anterior view of ventral valve, GSC 97049 from GSC loc. 53721, section 116H-1B. M, posterior view of ventral valve, GSC 97047 from GSC loc. 53721, section 116H-1B. N, lateral view of ventral valve, GSC 97147 from GSC loc. 53703, section 116H-1A. O, anterior view of ventral valve, GSC 97054 from GSC loc. 56972, section 116F-16. All specimens are in natural size.



Holotype. USNM 125339 figured in Cooper (1957) in pl. 5A, figs 2 and 3 from the Coyote Butte Formation, central Oregon, United States.

Diagnosis. Large transverse *Yakovlevia* with flattened to gently convex ventral visceral disc; sulcus and fold well developed at maturity; 5–7 costellae in 5 mm on ventral trail.

Referred material. Eight specimens with valves conjoined from GSC loc. 53703, section 116 H-1A; 6 conjoined specimens from GSC loc. 53721, section 116H-1B; 10 ventral valves and 5 dorsal external moulds from GSC loc. 53860, section 116P-10; 4 ventral valve and 1 dorsal external mould from GSC loc. 53862, section 116P-10; 1 ventral valve from GSC loc. 53946, section 116C-1; 5 ventral valves and 3 dorsal valves from GSC loc. 56972, section 116F-16; 3 ventral valves, 1 ventral internal mould, 3 dorsal external moulds, 4 dorsal internal moulds and 2 complete shell specimens from JBW loc. 88, near section 116F-16 (see Fig. 4 for locations of the GSC sections).

Description. Shell medium to moderately large with transverse outline; widest at hinge line. Ventral valve abruptly geniculated at angle between 60° and 80°; visceral disc flat to gently convex, subrectangular to trapezoidal in shape; umbo tiny, flat; no prominent umbonal slopes; ears large, well extended, but poorly differentiated from umbo, slightly to moderately rounded in cross section; hinge usually slightly wider than midwidth; cardinal extremities acute at 80° on average; angle between hinge margin and lateral margin of visceral disc ranging from 55° to 65°; trail approximately 1.5 as long as visceral disc when completely preserved, subquadrate to slightly concave distinct in all ventral specimens, but varying in depth and distance from umbo in specimens even from one locality, usually commencing 2–4 mm from umbo with sulcal angle at 40° to 50°, deepening and widening forwards, strongest over geniculation area with angular floor, slightly shallower anteriorly and floor more broadly rounded; flanks bounding sulcus high and narrowly rounded in transverse section with nearly vertical lateral slopes. Costellae well defined, low and rounded, 8 in 5 mm at 6 mm from umbo (Fig. 6M), 5–7 in 5 mm on trail (Fig. 6I), anteriorly increasing by intercalation, separated by narrow interspaces, slightly converging in sulcus in some specimens; rugae much weaker than costellae, low and rounded, 1–2 per mm, better defined on inner ears, slightly crossing costae; reticulation indistinct. Spines few, well differentiated; coarse strut spines usually measuring

1–1.5 mm in diameter, interrupting 2 or more costellae which continue forward in front of spine bases, slightly varying in number and position, but always with one pair from cardinal extremities, one and rarely two pairs on flanks bounding sulcus, none on lateral slopes, and rarely one in sulcus (Fig. 6L); finer spines comparatively more numerous, in row along hinge line and rare over trail and visceral disc, there arising from single costella, 0.5 mm in diameter.

Dorsal valve strongly concave, but visceral disc flat, trapezoidal; geniculation abrupt and narrow with angle between 50° and 75°; trail approximately as long as disc; fold variable as ventral sulcus, normally beginning at 3–5 mm in front of dorsal umbo, strongest over middle valve, crest rounded. Costellae similar to those on ventral valve; but rugae slightly stronger and more regularly defined, confined to visceral disc, about 5–7 in 5 mm, crossing costellae to form more prominent, at times well defined, reticulation in visceral disc; no spines observed on dorsal valves. Shell pseudopunctate, preserved as fine pits on worn surface (Fig. 6N).

Ginglymus not preserved; transverse band along posterior margin of both valves distinct in many specimens, 3–4 mm in diameter, irregularly pitted on ventral side and matched by tubercles on dorsal side, extending laterally across ears to lateral margins, there replaced by lateridges; lateral ridges striated and not reaching anterior margin.

Ventral muscle field deeply depressed just below transverse band, triangular in shape, posteriorly narrower and extending across transverse band, leaving small, smooth triangular opening simulating delthyrium, encircled by low ridges; adductor platform raised, high, narrow and elongate, divided by very thin median groove in some specimens, slightly striate on anterior portion, posteriorly smooth; large diductor scars on each side, deeply depressed below valve floor, flabellate, posteriorly smooth, anteriorly marked by distinct radial grooves and ridges; rest of valve floor densely granulate and pitted, stronger toward anterior margin.

Dorsal adductor scars small, slightly raised and dendritic, oval in shape; brachial ridges distinct with slightly recurved anterior portions, smooth inside loops; median septum low between adductor scars, extending slightly beyond midline ending with high anterior; floor irregularly granulate and pitted; 2–3 concentric rows of small endospines in front of brachial ridges and median septum.

Measurements. Width ranges from 30 to 47 mm, length 18 to 88 mm, height 15 to 19 mm, and cardinal angle 70° to 80°.

Comparisons. The holotype of *Yakovlevia transversa* (Cooper 1957) from the Coyote Butte Formation of central Oregon has a slightly deeper and longer sulcus than some of the Yukon specimens, but this feature is variable in the Yukon collections. Smaller specimens usually have a shallower sulcus (e.g. Fig. 6M). Larger and more transverse specimens possess a slightly deeper and longer sulcus (Figs 6J, O) comparable with that of the Oregon types. The two specimens figured as *Y. transversa* by Nelson & Nelson (1985) seem to be conspecific, but the ventral internal mould figured in their fig. 12 as the same species seems to have been mislabelled; it is perhaps a ventral internal mould of *Purdonella* Reed or ally, because it has long subparallel adminicula and a well impressed, elongate muscle field; this is not like any of the ventral interiors of *Yakovlevia transversa* from northern Yukon Territory.

Y. mammata (Keyserling 1846: p. 206, pl. 4, figs 5, 5a, b) and *Y. mammatiformis* (Fredericks 1926: p. 87, pl. 3, figs 4–6) are the two species closest to *Y. transversa*. The first was originally described from the possibly Sakmarian fauna of the Urals and has now been widely reported from chiefly Lower Permian (Asselian to Kungurian) in the Russian Arctic, Arctic Canada, and northeast China. The type material of this species is similar to some small specimens of the present species, with a shallow sulcus. Types of *Y. transversa* and most Yukon hypotypes are much larger and more transverse than *Y. mammata* and have a deeper sulcus. *Yakovlevia mammatiformis* from the Sakmarian beds in Kcjim Terovey River of Timan, appears to be closer to *Y. transversa* in general appearance. The Russian types are poorly preserved but do show a large size, a more transverse outline, and coarser, more widely spaced costellae (see Abramov & Grigor'yeva 1983: pl. 10, figs 13, 14).

Occurrences. In the northern Yukon Territory, *Y. transversa* occurs throughout the Jungle Creek Formation, but is most abundant in the *Yakovlevia transversa* Zone in the lower-middle part of the formation. Outside the Yukon Territory and apart from its occurrence at the type locality from the Coyote Butte Formation in central Oregon, *Y. transversa* is known also from the possibly Sakmarian fauna in southeast British Columbia (Nelson & Nelson 1985).

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